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RADULAR CONFIGURATION AND THE TAXONOMIC HIERARCHY IN THE ARCHITECTONICIDAE (GASTROPODA)

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ABSTRACT. The literature dealing with the radula in the Architectonicidae is reviewed and new observations are added both from microscopic and SEM examinations. Three subfamilial units are recognized; a list of species in which the radula is known, all herein described and illustrated, is conjoined: Architectonicinae: *Architectonica c.f. laevigata* (Lamarck 1822), *A. nobilis* Röding 1798, *A. perspectiva* (Linnaeus 1758), and *A. reevei* (Hanley 1862); Philippiinae: *Acutitectonica acutissima* (Sowerby 1914), *A. disca* (Philippi 1844), and *A. lepida* (Bayer 1942), *Philippia hybrida* (Linnaeus 1758), *P. lutea* (Lamarck 1822), *P. krebsii* (Mörch 1875), *P. oxytropis* (A. Adams 1854), and *P. radiata* (Röding 1798); Heliacinae: *Heliacus architae* (Costa 1830), *H. bisulcatus* (d'Orbigny 1842), *H. borealis* (Verrill and Smith 1880), *H. cylindricus* (Gmelin 1791), *H. dorsuosus* (Hinds 1844), *H. fallaciosus* (Tiberi 1872), *H. jeffreysianus* (Tiberi 1867), *H. perrieri* (Rochebrune 1881), and *H. trochoidea* (Deshayes 1830), *Pseudomalaxis nobilis* (Verrill 1885), and *Spirolaxis centrifuga* (Monterosato 1890).

Attempts to ascertain a proper taxonomic position for the Architectonicidae on the basis of its radular morphology were initially thwarted since researchers were unable to find a radula because of its small size and unusual position. The family was, thus, variously placed in aglossate groups, the Aglossa, and the Gymnoglossa (Gray, 1853a and b; Mörch, 1860).

MacDonald (1860: 76–77) was the first to discover and describe the jaws and radula of an architectonicid and he recognized, in the case of *Solarium* [=*Architectonica*] *perspectivum*, a ptenoglossate condition similar to the Epitoniidae and Janthinidae. He described the species as follows:

> The oral teeth [=jaws] form a narrow circular band consisting of a pavement of sharp dental cells, whose points, as in other cases, are directed forwards.
>
> The lingual pavement [=radula] is small, but elongated in form and divided into two lateral areas, supporting several series of long and gracefully curved uncinate teeth, which seem to decrease in length from within towards the lateral borders of the membrane, where they also become bifid in the vertical direction.

Troschel (1861) was the first to figure the radulae and jaws for architectonicids. For *Solarium* [=*Architectonica*] *perspectivum* he counted at least 60 rows of long, narrow teeth (Pl. 47, figs. 1–5) and found that each row has a total of 28 teeth (Pl. 47, fig. 12) and concluded, since he could find no central tooth, that there was none. Therefore, the radula formula is 14-0-14. The lateral teeth are prong-like with the longer ones central or medial in position and the shorter at the margin of the radula (Pl. 47, fig. 1). The longer ones have simple pointed cusps (Pl. 47, fig. 5) while those somewhat more lateral in position, though still prong-like, have a small lateral cusp along shaft of the tooth (Pl. 47, figs. 8 and 11a); the more marginal laterals are not only shorter but the small cusp mentioned above becomes longer (Pl. 47, fig. 2); Troschel likened these teeth to a fork with unequal tines. He also illustrated the lateral teeth in a view so one could not see the small tines clearly (Pl. 47, fig. 3). These teeth measure from 0.06 mm to 0.2 mm in length. He described the jaw of *A. perspectiva* (Pl. 47, fig. 6) as consisting of lancet-like elements arranged like tiles on a roof though not perfectly regular; the free edge is irregular with some of the pointed rod-like elements projecting; these elements measure 0.0075 mm broad by 0.0275 mm long.

Troschel (1861; 1875) could only observe portions of the radula of *Philippia lutea* [=*P. hybrida,* since his specimen was from the Mediterranean Sea]. He noted the presence of numerous teeth, thereby relating it to *Solarium* [=*Architectonica*] but he never gave a radular formula, nor specifically noted the presence or absence of a central tooth though he implied there was no central tooth. He clearly illustrated the lateral teeth as having from two to three prong-like cusps (Pl. 47, fig. 7); however, the dental elements he mentioned as central, or in the middle, in position (Pl. 47, fig. 9) are confusing and probably represent some error in judging the preparation. He observed that the jaw of *P. hybrida* has bluntly rounded, rod-shaped elements which are about four times longer than broad and arranged in 4–6 irregular rows, somewhat like roof tiles (Pl. 47, fig. 10).

Troschel (1875) recounted his earlier work on *Architectonica perspectiva* and studied the radula of another specimen, one from the Philippines which though labelled *Solarium zonatum* he equated to *A. perspectiva.* The angles of the recurved tines of the more marginal lateral teeth (Pl. 47, figs. 11b, c, d) differ somewhat from the specimen he previously figured in 1861 (Pl. 47, figs. 2 and 4). However, the essentials are the same.

Troschel (1875: 157) in an addendum, discussed *Torinia* [=*Heliacus*] *cylindracea.* Although he had difficulty with his preparation because of the minuteness of the radula and was uncertain of the completeness of his observation since the teeth had become disassociated, he could still surmise that the radula of *Torinia* [=*Heliacus*] is a modified taenioglossate one with five teeth per row, giving the formula 2-1-2—two laterals flanking a central tooth. He said the central tooth (Pl. 48, fig. 1) is almost rectangular in shape with the cutting edge consisting of a single central cusp flanked on each side by about 14 rather deeply incised, very narrow cusps. Both lateral teeth are narrow and basally blunt, widened distally and having deeply cleft, finger-like cusps, seven on the inner lateral and eight on the outer (Pl. 48, fig. 2). The central tooth measures 0.08 mm by 0.05 mm. Because of the presence of the central tooth and the limited number of lateral teeth in *Torinia* [=*Heliacus*], he established

a new family, the Toriniacea [=Heliacidae] and separated it from the Soliariacea [=Architectonicidae] in which he placed *Solarium* [=*Architectonica*] and *Philippia*.

Marshall *in* Tryon (1885) reproduced Troschel's figures for *Solarium* [=*Architectonica*] and *Philippia* and stated that the teeth "are long, spiniform, pronged and without central tooth." For *Torinia* [=*Heliacus*], he noted "there is a small central tooth, a lateral tooth with pectinated and incised edge united to the central tooth and two marginal teeth which are straight and digitated at their extremities."

Bouvier (1886: 99 and 105) recounted Troschel's (1875) observations on the radula and jaws of *Solarium* [=*Architectonica*], noting that the laterals are numerous, spiniform and terminating in one, two or three cusps. Discussing the radula of *Torinia* [=*Heliacus*], he correctly noted the central tooth with its large central cusp bordered by numerous small cusps and the lateral teeth with their six or seven terminal cusps though he incorrectly stated that there were six lateral teeth per row, the true taenioglossate condition, instead of four.

Thiele (1925) made rather extensive comments on the radular configuration of the Architectonicidae. He rightly pointed out Marshall's (1885) incorrect interpretation of the dental elements of *Torinia* [=*Heliacus*], that his "central tooth" and "lateral tooth" really are, respectively, the central knobby cusp and lateral, finely denticulated cusps of the central tooth. He contrasted the radulae of *Torinia* [=*Heliacus*], *Philippia,* and *Architectonica* referring to Troschel (1875) for *Torinia.* He figured (Pl. 48, fig. 3) the central tooth of *Torinia* [=*Heliacus*] *trochoidea.* This is a side view rather than the usual frontal view but still shows the heliacine configuration of the central tooth—a central cusp flanked by numerous (here 15) fine lateral cusps. The lateral teeth are narrow and distally broadened, terminating in several adjacent finger-like long, narrow, curved cusps of which the outermost are broadest and shortest. He found, after having examined different species, that the form of the lateral teeth in *Torinia* [=*Heliacus*] varies as does the number of cusps,

between six and ten. He was the first to figure the jaw of a heliacid—*Torinia* [=*Heliacus*] *trochoidea*; it is narrow and made up of adjacent pointed, slightly curved little rods on which sometimes a second point is found (Pl. 48, fig. 6).

Thiele (1925) also had difficulty in isolating the minute radula of an unnamed species of *Philippia,* but he noted that there were five teeth per row though not explicitly stating but inferring the presence of a single central tooth and two pairs of laterals. The lateral teeth are not greatly differentiated, being narrow and terminating mostly in three but sometimes two thin cusps; however, a closer examination of his illustration indicates a frontal view of a central tooth (Pl. 48, fig. 4) with its single median pointed cusp flanked by the longer pointed, thin lateral cusps and a side view of one lateral tooth (Pl. 48, fig. 5) with its recurved form and three slim, narrow pointed cusps. He found that the jaw rods of *Philippia* gradually taper to points on their free edges (Pl. 48, fig. 7). [This does not conform with Troschel who showed them to be rather bluntly rounded, Pl. 47, fig. 10]. Thiele went on to consider that *Philippia* was an intermediate between the more primitive *Torinia* [=*Heliacus*] and the more derived *Architectonica* with its numerous single and double pronged teeth; he concluded that the family Architectonicidae was not ptenoglossan and therefore, not related to the scalids [=epitoniids] or janthinids, but to the Mathildidae.

Thiele (1926) figured an individual long, narrow, pointed lateral tooth of *A. perspectiva* (Pl. 47, fig. 13), remarking only that the genus had numerous teeth, sometimes with a secondary cusp. He recognized *Heliacus* as having five teeth per row with a strong central tooth and two narrow, distally sharply denticulate lateral teeth and *Philippia* with only a few teeth, without giving a specific number. He formalized the separation of the family from the Ptenoglossa, placing the Architectonicidae next to the Mathildidae in the Cerithiacea.

Thiele (1928) described and figured the central and lateral teeth of what he called *Philippia hybrida*. He characterized the central tooth as strongly formed, long and narrow with a short strong hook or central cusp flanked on either side by two bristle-like appendages or cusps, "borstenartigen An-

hangen" (Pl. 48, figs. 8 and 9); the inner lateral tooth has four, the outer five, long, thin, also bristle-like cusps (Pl. 48, figs. 10 and 11, respectively); he then stated that *Philippia,* by its radular structure is closer to *Torinia* [=*Heliacus*] than to *Solarium* [=*Architectonica*], because in the latter the number of teeth is much increased and some of the lateral ones are simply pointed while others are forked (Pl. 48, fig. 12).

Thiele (1929), summarizing the features of the family, stated the radular formula of *Solarium* [=*Architectonica*] as 14-0-14 with the central tooth being absent and the lateral teeth longer and singly pointed more centrally, and shorter and forked more laterally. He characterized *Torinia* [=*Heliacus*] as having five teeth per row, describing the central and lateral teeth as previously known, and then for the first time noted that *Philippia* also has five teeth per row with a central tooth not broader than the lateral teeth and bearing bristle-like projections ("borstenartigen Fortsätzen") on the cutting edge; the lateral teeth are like *Torinia* with several cusps.

Habe (1943), working on *Heliacus dorsuosus,* illustrated the central tooth with its median cusp flanked by numerous lateral serrations (Pl. 49, fig. 3) and both lateral teeth, in this case, each with nine narrow, digitate cusps (Pl. 49, figs. 1 and 2).

Habe (1952) illustrated three odd structures, each having three long spiniform cusps, which he considered with no explanation to be the radula of *Discotectonica* [=*Acutitectonica*] *acutissima* (Pl. 58, fig. 2); we think that this is a separate structure and consider it subsequently.

Robertson (1970) reviewed the literature on the radula of *Philippia,* remarking that Troschel's (1861) *P. lutea* was *P. hybrida* and that Thiele's (1925) *P. hybrida* was really *P.* (*Psilaxis*) *radiata* since the name *P. hybrida* was at that time (Thiele 1925; 1928; 1929) being applied to *P. radiata.* He stated that Troschel (1861; 1875) was wrong in believing that *Philippia hybrida* has about as many teeth as *Architectonica* (*i.e.* about 28). In point of fact, Troschel said he had a difficult time manipulating the tiny radula and that he could only make out single teeth or parts of the radula; he was not

able to give an exact number of teeth in *Philippia;* he only remarked that the teeth were numerous and similar to *Architectonica* in their general arrangement. Robertson also found that the radula was difficult to study and stated that, for *Philippia,* there were no subgenerically distinguishing characters. Robertson extracted radulae from six specimens representing four species and gave measurements for the length and height of the radula, the number of rows of teeth and the size of the shell. For four species the radular length varied from 0.33 to 1.4 mm and the number of rows of teeth from 29 to 58. Robertson noted that the "narrow and bilaterally symmetrical teeth are densely packed together... and their bases are positioned in an irregular diagonal pattern across the ribbon." He described the philippiine radula in general using *P. radiata* as an example. We have reproduced his figures 9 B–D as our Pl. 49, figs. 4–6. Robertson said: "I think it more likely that the innermost teeth are the ones that are smallest, narrowest, and singly pointed (fig. 9A). The other two kinds of teeth differ in length, thickness, curvature, and the number of distal spines. The longer ones (fig. 9B) have two or three spines, while the shorter ones are laterally thicker and more curved and have three to six spines (fig. 9C). One of the latter teeth, definitely not from the center of the radula, in frontal view (fig. 9D) resembles Thiele's figure (1928, p. 87) of a *Psilaxis* 'central' ". He also said there appeared to be five teeth per row, but was unable to discern the arrangement of the teeth on the radula—whether there were consistently five in a row or if they were variable or even asymmetrical. It is obvious that Robertson misinterpreted his data as will be clearly shown by Melone's (1974) work with species of *Philippia* (*Philippia*) *hybrida* and Climo's (1975) analysis of *P.* (*Psilaxis*) *oxytropis.* Robertson stated that the jaws differed between the subgenera *Philippia* and *Psilaxis.* The species referable to *P.* (*Philippia*) *hybrida* are subcircular while those in *P.* (*Psilaxis*) (*e. g. krebsii, oxytropis* and *radiata*) have jaw rods that are elongate. This may be the reason he thought Troschel's 1861 *P. lutea* was *P. hybrida* since Troschel figured bluntly rounded, rod-shaped elements about four times longer than broad (Pl. 47, fig. 10) while Thiele (1925)

showed them for *P. hybrida* (=*radiata*) to be rather bluntly rounded and tapering to points on their free edges (Pl. 48, fig. 7).

Melone (1974) described and illustrated with excellent SEM photographs the radulae of two species of philippiines and two species of heliacines. Now for the first time one can see clearly in full three-dimensional aspect the shapes, sizes and positions of various architectonicid radular teeth. Melone kindly sent us a superb set of these photomicrographs which he used in this study, some of which are reproduced in Plates 50 to 53. We take this opportunity to extend our thanks for his cooperation.

Melone (1974) discussed and figured the radula of *Philippia hybrida* (Pl. 50, figs. 1 and 2); it consists of five teeth per row with a formula 1+1+R+1+1 where R equals the rachidian or central tooth, plus a lateral and marginal tooth on each side. The central tooth measures 90.0 u in length and 6.0 u in breadth with a long digitiform spine or cusp on either side of the shorter central cusp; the central cusp measures 15.0 u × 1.5 u and the outer cusps 35 u × 2.5 u; the lateral and marginal teeth are 100 u by 6 u and have three sharp digitiform distal cusps [it appears to us that there are only two cusps on the outer lateral tooth]. He also worked with the radula of *Architectonica mediterranea* [=*Acutitectonica lepida*] (Pl. 53, figs. 1 and 2); it consists of five teeth per row with an elongate, narrow, prong-like smoothly knobbed central tooth measuring 150 u × 12 u flanked by a lateral and marginal tooth on each side which terminate in seven fine, curved, and pointed cusps; the lateral and marginal teeth measure 160 u × 12 u. He remarked that the radula of this species is very similar to that of *Architectonica nobilis* for which he has unpublished data and for this reason a systematic revision of the genus *Architectonica* is required.

Also Melone (1974) described and illustrated the radula of *Heliacus architae* (Pl. 51, figs. 1 and 2). The central tooth is narrow and long (32 u × 15 u) and it terminates in a single simple median cusp (17 u × 3 u) which is flanked by 13–15 smaller short (1 u) dentiform cusps; the inner and outer lateral teeth (65–70 u × 8 u) have several (6) spiniform processes; the lateral teeth tend to arch over the smaller

central tooth. He similarly portrayed the radula of *Heliacus fallaciosus* (Pl. 52, figs. 1 and 2); the central tooth is 90 u long and 7 u wide, distally recurved and terminating in a single simple median cusp about 22 u long and 3 u wide which is flanked by 18–20 small spiniform cusps or denticulations (about 1 u in width); the inner and outer lateral teeth (134 u × 10 u) have 9–10 spiniform processes on the inner and only six on the outer tooth; Melone remarked that *H. fallaciosus* is obviously congeneric with *H. architae.*

Melone (1975) described and figured what he considered to be the radula of *Acutitectonica acutissima* (Pl. 54, figs. 1–3); we have reason to believe that this is a specialized structure and discuss it subsequently.

Recently Climo (1975) examined and illustrated the radula of *Architectonica reevei* (Pl. 49, figs. 7–10). He found 27 rows of teeth, each row consisting of seven laterals on each side of a central tooth, thus giving the formula 7–1–7. The central tooth was more "robust" than the laterals and tricuspid with the central cusp flanked by smaller lateral cusps. All lateral teeth were strongly curved and forked with long tapering subequal cusps; the two more medial lateral teeth are the longest. Climo was incorrect in stating that Troschel (1875: 156) did not mention the central tooth in *A. perspectiva* since Troschel explicitly remarked "Die Radula ohne Mittelplatten...". Further, Climo suggested that: "It appears likely that *Architectonica perspectiva,* like *A. reevei,* has a central tooth; it just has not been recognized yet." He related the reduction in the number of lateral teeth in *A. reevei* to its comparatively smaller adult shell size [up to 30 mm in diameter] than *A. perspectiva* [up to 70 mm in diameter]. He noted that the radula of *A. reevei* shows similarity to *Philippia* in the presence of a tricuspid central tooth; however, it does not have the two multicuspid marginal teeth on each side of the central tooth as in *Philippia.* He also said that in contrast to *A. perspectiva,* it differs in having a central tooth and in having all its lateral teeth bicuspid.

Climo (1975) also reported on the radula of *Philippia* (*Psilaxis*) *oxytropis* (Pl. 49, figs. 11–14) describing it thus:

With formula 2–1–2. Central tooth about as long as outer marginal, curved, with a posteriorly-projecting basal buttress; tricuspid, the central cusp more robust than the two outer, and more curved causing lateral cusps to lie above it when tooth is viewed in profile; cusps much shorter than on marginal teeth. Inner marginal tooth tracing a long, sigmoid curve in profile with three long, curved cusps, the apical one longest and set a little apart from the outer two; basal portion wide with a curved locking buttress. Outer marginal shorter than inner, crown more curved and with four or five cusps, equal in width but in a decreasing length series from apex; about same length as central tooth.

Investigating the radula of 14 species, most of which were previously unknown anatomically, Merrill (1970) confirmed, in his comprehensive but unpublished dissertation on the family Architectonicidae, many previous observations and contributed much new information on the radula. We are herewith incorporating his data into this text and augmenting it by our more recent analyses.

The Indo-Pacific species, *Architectonica perspectiva,* has a radula up to 2 mm in length with the formula 14–0–14. We find that there is no central tooth in this species, confirmed both by light and scanning electron microscopy (Pl. 56, fig. 1a–e; Pl. 63, fig. 2; Pl. 64, figs. 1–3). The lateral teeth are long and prong-like, with the two marginal ones being shorter, forked and bicusped; these teeth measure 0.05 mm to 0.25 mm in length, in very close concordance with Troschel's (1861: 96) measurements. Occasionally there is an anomalous placement of sharply bicuspid lateral teeth (Pl. 64, figs. 2 and 3) placed at some distance inward from the margin of the radula; the difficulty in counting the number of teeth per row is indicated by the jumbled, entanglement of the teeth (Pl. 64, fig. 1). The related *A. nobilis,* a west Tethyean species, has 60–70 rows of teeth with only 14 teeth in a transverse row and is thought to be without a central tooth, thus giving a formula of 7–0–7 (Pl. 56, fig. 2a–c; Pl. 63, fig. 1). The prong-like centrally disposed teeth are long up to 0.2 mm in length and with a single cusp while the single outer marginal tooth is short about 0.05 mm in length, forked and bicusped. In our SEM preparation (Pl. 65, fig. 1) certain elements were present in the central field of the radula (Pl. 65, fig. 2) which might be construed as being a central tooth because they are so placed and appear to be morphologically differentiated from the

elongately cusped lateral teeth; that is they have short, pointed cusps. Although we are unable to confirm the presence of these elements by conventional microscopy we cannot be certain if the radular formula of *A. nobilis* is 7–0–7 or 7–1–7. The jaws of both *A. perspectiva* and *A. nobilis* are made up of numerous pointed rods (Pl. 56, figs. 1b and 2b). SEM analysis of the jaws of *A. nobilis* confirms the pointed configuration of the jaw rods (Pl. 67, fig. 1) and shows an unusual hexagonal pattern on the base of the jaw (Pl. 67, fig. 2). The radula of *Architectonica c.f. laevigata* from the Indo-Pacific is less than 1 mm in length (Pl. 66, fig. 1) and has a short pointed central tooth and seven lateral teeth on each side; the lateral teeth are recurved, prong-like and forked with long, tapering subequal cusps (Pl. 66, figs. 2 and 3); thus, the radular formula is 7–1–7.

The genus *Philippia,* on the basis of several well-defined shell characters, has been subdivided taxonomically into *Philippia s.s.* and *Psilaxis.* The radula of *P.* (*Philippia*) *lutea,* type species of the genus, (Pl. 57, fig. 1d) of the Indo-Pacific compares closely to that of *P.* (*Philippia*)*hybrida* of the eastern Atlantic (Pl. 50, figs. 1 and 2; Pl. 65, fig. 3); it has five teeth per row with the formula 2–1–2; the radula is about 0.5 mm in length and 0.1 mm in breadth. Characteristically the central tooth which may attain a length of about 0.07 mm, has a narrow central or median cusp flanked on each side by a long filiform cusp (Pl. 65, fig. 3). The inner lateral tooth has three, the outer lateral two cusps (Pl. 57, fig. 1f). The Atlantic *P.* (*Psilaxis*) *krebsii*, type species of the subgenus, has a radular formula of 2–1–2 with five teeth per row and about 32 rows (Pl. 57, fig. 2a–d). The central tooth, which may attain 0.07 mm in length, has a strong, somewhat knobby central cusp bordered by a slender pointed cusp on each side. The inner lateral tooth has five sharp spiniform cusps while the outer lateral has three cusps. The jaws of *P. lutea* and *P. krebsii* are similar in consisting of rounded, pointed rod-shaped elements (Pl. 57, figs. 1a and 2a). Robertson (1970) noted a subgeneric difference in the shape of the jaw elements, those of *Psilaxis* being elongate and those of *Philippia s.s.* being subcircular. Our observations and illustrations (Pl. 57, figs. 1a and 2a) do not indicate the differences described which seemed clear to Robertson. Our

SEM observation of the jaws of *P. hybrida* confirms the pointedness of the rods and also shows them to have a medial longitudinal furrow (Pl. 68, fig. 1); the basal portion of the jaw exhibits a pattern of papillose knobs (Pl. 68, fig. 2).

Acutitectonica disca has a radula up to 0.75 mm in length with five teeth per row, giving the formula 2–1–2; the central tooth, up to 0.10 mm in length, is long, slender with a simple knobby, somewhat bulbous distal portion (Pl. 58, fig. 1c and d); the inner and outer lateral teeth have up to eight cusps (Pl. 58, fig. 1c–e). The rod-like jaw elements are blunt (Pl. 58, fig. 1b).

Additionally in the esophagus of *A. disca* there is a long, slender and rod-like cuticularized structure about 0.10 mm in diameter along which at regular intervals of about 0.10 mm are found pairs of three spined or pronged recurved appendages, two on each side of the rod or four to the row (Pl. 58, fig. 3; Pl. 55, figs. 1–4). Habe (1952) illustrated similar small recurved hooked portions mistaking them for the radula of *A. acutissima* (Pl. 58, fig. 2). Melone (1975) examined a specimen of *A. acutissima* and also misconstrued this rod-like structure as a radula. Illustrated with fine SEMs (Pl. 54, figs. 1–3) he showed the structure to be between 7–10 mm in length and about 0.20 mm in width with pairs of three pronged recurved elements disposed at about 0.15 mm intervals. He considered each row of these elements as consisting of a pair of lateral and marginal teeth separated by a minute central dental element and, thus , gave a formula of 1–1–R–1–1. The lateral and marginal elements have essentially the same morphology and are indeed reminiscent of lateral teeth, consisting of a subtriangular, anteriorly recurved and posteriorly projecting arcuate lamella with three very long posteriorly pointed cusps. The median element or "central tooth" consists merely of a tiny uncinus. Since we found both a similar structure (Pl. 55, figs. 1–4; Pl. 58, fig. 3) and the true radula (Pl. 58, fig. 1) in the esophagus of *A. disca,* it must be considered as an independently derived and accessory feature in the alimentary canal of *Acutitectonica;* its function remains unknown but presumably it is associated with feeding.

We consider below five species of *Heliacus* and one each of *Pseudomalaxis* and *Spirolaxis*. Although each species has slight differences in detail, the basic radular configuration is a modified taenioglossate pattern with five teeth per row, the formula being 2-1-2; the central tooth has a median cusp or knob flanked on each side by numerous short spines or fine denticulations; the lateral teeth are strong with two to eight more or less spiniform cusps. Details of each species are given in the following descriptions.

In *Heliacus cylindricus* the central tooth is broad, about 0.08 mm long, and has a narrow median knob or cusp flanked by numerous lateral spiniform cusps (13–14) extending on the outer edge of the fold on either side; the lateral teeth have about five spines and are up to 0.13 mm in length (Pl. 59, fig. 1). These observations of *H. cylindricus* compare favorably in most respects with those of Troschel (1875) on the same species (contrast Pl. 48, figs. 1 and 2 with Pl. 59, fig. 1), namely in the length and shape of the central tooth as well as in the number of small lateral cusps on either side of the central knobby cusps. The radula of *H. perrieri* (Pl. 59, fig. 2) is quite similar reaching a length about 1.00 mm with a narrow central tooth about 0.03 mm in width with its median cusp flanked by nine to ten deeply cleft cusps; the lateral teeth about 0.12 mm in length have up to seven finger-like cusps. The jaw elements of *H. cylindricus* and *H. perrieri* are regularly or irregularly pointed though larger and more craggy in the latter (Pl. 59, figs. 1a and 2a).

The radula of the *Heliacus jeffreysianus* (Pl. 60, fig. 1) has a narrow, somewhat cowled central tooth, about 0.03 mm in length and 0.006 mm in width, having a rather triangular spiniform median cusp bordered by numerous (10–12) serrations; the narrow lateral teeth, about 0.03 mm in length and 0.005 mm in width, have up to eight sharply pointed finger-like cusps. In *Heliacus borealis* (Pl. 60, fig. 2) the radular ribbon which is about 0.4 mm in length, has nine rows of regularly spaced teeth; the central tooth, about 0.12 mm in length and 0.02 mm in width, bears a median triangular spine or cusp which is bordered on each side by about 12 narrow spines which are longer nearer the central

cusp and become shorter distally; the long narrow (about 0.11 mm by 0.01 mm) inner and outer teeth have several spiniform cusps. The jaw rods are somewhat irregular in shape and distally pointed (Pl. 60, fig. 2a).

The shells of *Heliacus bisulcatus* and *H. architae* were each under 5 mm in greatest diameter making it difficult to manipulate the tiny radulae into suitable positions to see salient features clearly if at all. The radula of *H. bisulcatus* (Pl. 61, fig. 1) is narrow, about 0.01 mm in width and has a cowled central tooth with a short, knobby median cusp flanked by 6–8 short rather blunt or knobby denticulations on its inner fold or cutting edge; the lateral teeth, up to 0.09 mm in length, have 6–8 finger-like cusps while in the related *H. architae* (Pl. 61, fig 2) the central tooth is somewhat broad in comparison to its length, only 0.01 mm in width, with a subtriangular median cusp flanked by about eight blunt cusps; the lateral teeth, up to 0.05 mm in length, bear two or three curved spine-like cusps. The rod-like jaw elements are pointed (Pl. 61, fig. 1b). With the greater resolution of the scanning electron microscope, Melone (1974) had very similar length measurements for the central and lateral teeth of *H. architae* (Pl. 51); the width of the central tooth is 15 u versus ours of 0.01 mm and the width of the lateral teeth is betwen 65–70 u against ours of 0.05 mm; he could more clearly discern the numbers of lateral cusps on each side of the central cusp of the central tooth (13–15) instead of our eight and for the lateral teeth (six) instead of our two to three.

In *Pseudomalaxis nobilis,* the radula (Pl. 62, fig. 1) has a basally broad, about 0.023 mm, central tooth narrowing to a beak, about 0.013 mm, as a distal cusp bearing projection; its median or central cusp, is bordered laterally with numerous (up to 20) sharply pointed serrations; the lateral teeth, which are about 0.08 mm in length and 0.008 mm in width, are rather strongly curved distally and bear four finger-like pointed cusps.

In *Spirolaxis centrifuga* (Pl. 62, fig. 2) the radula has a central tooth which is broad and rectangular, about 0.013 mm in width and 0.02 mm in length, with a median cusp flanked by four denticulate lateral cusps; the lateral teeth are narrow, about 0.07 mm by 0.002 mm, and each have two

spiniform, finger-like cusps. A unique feature of this species is the configuration of the jaws which consist of numerous, elongate, multi-cusped strap-like plates (Pl. 62, fig. 2a).

Conclusions

From the preceding review of the literature plus our added work on the radula of the Architectonicidae, we postulate that the family is divisible, by its radular configuration into three principal groups, herein ranked as subfamilies (Architectonicinae, Philippiinae, Heliacinae) and thus confirming, with slight modifications, the earlier opinions of Thiele (1925), Merrill (1970), and Boss (1982).

The Architectonicinae are known by the structure of the radula of four species, *Architectonica perspectiva, A. nobilis, A. reevei,* and *A. c.f. laevigata,* having respectively the radular formulae, 14-0-14, 7-0-7 (or 7-1-7), 7-1-7, and 7-1-7; they are thus characterized by having numerous lateral teeth. Climo's (1975) description of the radula of *A. reevei* is important in at least two respects; its configuration links the purely ptenoglossate condition with the modified taenioglossate one found in both the Philippiinae and Heliacinae, and its central tooth has a shape like the Philippiinae, providing another transition between the Architectonicinae and Philippiinae. Further, both *Architectonica reevei* and *A. c.f. laevigata* (compare Pl. 49, figs. 9 and 10 and Pl. 66, figs. 2 and 3) have seven similarly forked bicuspid lateral teeth on either side of the central tooth, giving both the same radular formula; however, the central tooth of *A. c.f. laevigata* is comparable to that of the philippiine *Acutitectonica* (see Pl. 66, figs. 2 and 3 and Pl. 53, figs. 1 and 2) while the central tooth of *A. reevei* is like that of the philippiine *Psilaxis* (see Pl. 49, figs. 7 and 8 and Pl. 57, fig. 2d). Conchologically the species differ somewhat with *A. reevei* having a shell more similar to that of the Philippiinae and *A. c.f. laevigata* having a shell more closely resembling the Architectonicinae. Melone's (1974) undocumented assertion that *A. nobilis* has a radula very much like *Acutitectonica* which has only five teeth per row is unwarranted since *A. nobilis* clearly has numerous lateral teeth.

For the Philippiinae, the radula has five teeth per row, giving the formula 2-1-2 with the central tooth being a long narrow structure. Climo (1975) pointed out Roberston's (1970) errors in interpreting the radula of *Philippia* and substantiated the presence of a central tooth as noted by Thiele (1925) and Melone (1974). Although Robertson (1970) did not believe that the subgenera of *Philippia* could be distinguished by their radulae; such is not the case since *Philippia s.s.* has a central tooth with a narrow central cusp flanked by long filiform lateral cusps while *Psilaxis* has a central tooth with a knobby central cusp flanked by short cusps. *Acutitectonica* is also distinguished by its radular features, namely the central tooth is a simple naked knob, that is to say, a single cusped structure without lateral cusps. This radular character along with its conchological features serves to separate it at the generic level. The unique cuticularized esophageal structure in *Acutitectonica* further separates it from *Philippia.*

One unresolved problem concerns Thiel's (1927; 1928) illustration of the central tooth of what he called *Philippia hybrida* which Roberston (1970) referred to as *P. radiata.* This is the presence of the two bristle-like cusps on either side of the blunt, knobby central cusp (Pl. 48, figs. 8 and 9). Although Robertson (1970) stated that his lateral tooth of *P. radiata* (Pl. 49, figs. 5 and 6) resembled Thiele's figure of a central tooth, he did not mention that Thiele's figure had two pairs of bristle-like cusps while his only had one pair. His figure of the central tooth of *P. radiata* appears just like the other radularly known species of the subgenus *Psilaxis, e.g. P. oxytropis* and *P. krebsii,* which have only one cusp on each side of the knobby central cusp of the central tooth.

It might be added that the jaws of the Architectonicinae and the Philippiinae may differ in that *A. nobilis* has a hexagonal pattern discernible on the base of the jaw while in *P. hybrida* there are numerous papillose knobs.

Little controversy surrounds the characterization of the radula of the Heliacinae as exemplified by the type species of *Heliacus, H. cylindricus,* with its formula of 2-1-2. The central tooth, which shows a considerable range of variability in shape in the subfamily, is reminiscent of many

taenioglossate mesogastropods, in having a median or central cusp or knob flanked by numerous, fine lateral denticulations; the lateral teeth are multicusped with the inner lateral tooth larger and usually with more cusps. Although *Pseudomalaxis* and *Spirolaxis* have been treated previously in their own subfamily, the Pseudomalaxinae (Garrard, 1978), we note that neither the radular structures or conchological features are sufficient to distinguish them from the Heliacinae. We recognize *Spirolaxis* at the generic level because of its unique synapomorphy, the strap-like jaws. Of genera we consider referable to the Heliacinae, only the radula of *Awarua,* which we construe as conchologically intermediate between *Pseudomalaxis* and *Heliacus* remains unknown.

Abbreviations

ANSP—Academy of Natural Sciences, Philadelphia, Pa.
BCF—Bureau of Commercial Fisheries, Pascagoula, La.
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Ma.
USNM—National Museum of Natural History, Washington, D.C.
UZM—Universitetets Zoologiske Museum, København

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PLATES 47—68

Plate 47

Figs. 1–6 and 11–13. *Architectonica perspectiva*. Figs. 7–10. *Philippia hybrida*.

Fig. 1. Portion of radular ribbon to show forked lateral teeth in more marginal position (after Troschel 1861, fig. 4).

Fig. 2. Lateral teeth viewed to show cusps or tines (after Troschel 1861, fig. 7).

Fig. 3. Lateral teeth viewed so cusps or tines not easily discerned (after Troschel, 1861, fig. 8).

Fig. 4. Marginally positioned lateral tooth (after Troschel 1861, fig. 6).

Fig. 5. Most medially positioned lateral tooth without cusps (after Troschel 1861, fig. 4).

Fig. 6. The jaw with its pointed rod-shaped elements (after Troschel 1861, fig. 3; 1875, fig. 4a).

Fig. 7. Lateral teeth with two and three pronged cusps (after Troschel 1861, fig. 12; 1875, fig. 5e).

Fig. 8. Lateral teeth along length of row with tiny cusp on shaft (after Troschel 1861, fig. 5).

Fig. 9. Centrally located dental element (not representative) (after Troschel 1861, fig. 11; 1875, fig. 5b).

Fig. 10. The jaw with its roundly pointed, rod-shaped elements (after Troschel 1861, fig. 10; 1875, fig. 5a).

Fig. 11a–d. Individual lateral teeth of the radula (after Troschel 1875, Pl. 15, figs. 4c, d, e, and f) showing *a*, a more centrally disposed tooth larger in size and with a minute cusp on the shank and *b, c,* and *d* progressively more marginally positioned lateral teeth showing proportionate increase in distinctness of the two prong-like cusps.

Fig. 12. A complete half row of the radula (after Troschel 1875, Pl. 15, fig. 4b), the long uncusped lateral teeth being medial in position.

Fig. 13. Individual radular tooth (after Thiele 1926, fig. 52).

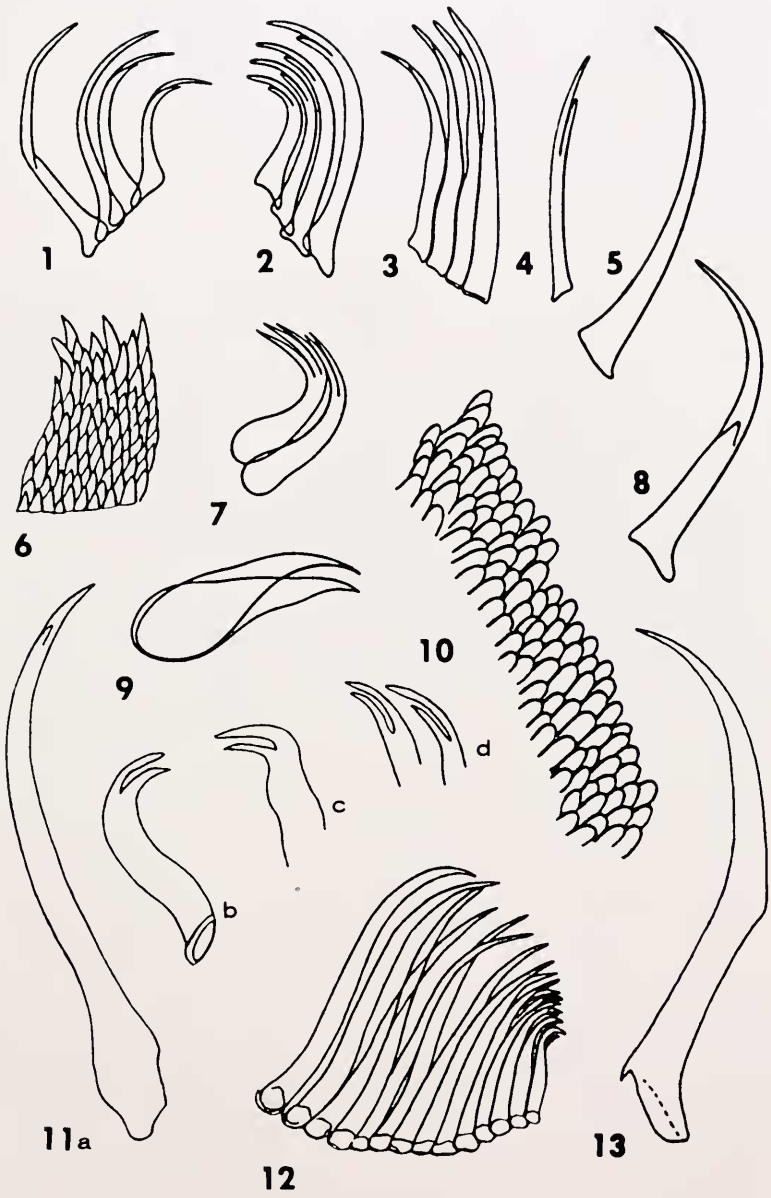

Plate 47

Plate 48

Fig. 1. The central tooth of *Torinia* [=*Heliacus*] *cylindracea* with central or medial knobby cusp and numerous fine lateral denticulations (after Troschel 1875, fig. 7a).

Fig. 2. The two lateral teeth of *Torinia* [=*Heliacus*] *cylindracea* with seven cusps on the inner lateral and eight on the outer lateral (after Troschel 1875, fig. 7b and c).

Fig. 3. Lateral view of the central tooth of *Torinia* [=*Heliacus*] *trochoidea* (after Thiele 1925, Pl. 46 [34], fig. 16).

Fig. 4. Frontal view of the central tooth of *Philippia* (after Thiele 1925, Pl. 46 [34], fig. 18 *pars*).

Fig. 5. Lateral view of the lateral tooth of *Philippia* (after Thiele 1925, Pl. 46 [34], fig. 18 *pars*).

Fig. 6. Jaw rods of *Torinia* [=*Heliacus*] *trochoidea* (after Thiele 1925, Pl. 46 [34], fig. 17).

Fig. 7. Jaw rods of *Philippia* (after Thiele 1925, Pl. 46 [34], fig. 19).

Fig. 8. Lateral view of the central tooth of *Philippia hybrida* (after Thiele 1928, fig. 8).

Fig. 9. Frontal view of the central tooth of *Philippia hybrida* (after Thiele 1928, fig. 8).

Fig. 10. Inner lateral tooth of *Philippia hybrida* (after Thiele 1928, fig. 8).

Fig. 11. Outer lateral tooth of *Philippia hybrida* (after Thiele 1928, fig. 8).

Fig. 12. Two lateral teeth of *Architectonica* (after Thiele 1928, fig. 9).

Plate 48

Plate 49

Fig. 1. The outer lateral tooth of *Heliacus dorsuosus* (after Habe 1943, fig. 5 *pars*).

Fig. 2. The inner lateral tooth of *Heliacus dorsuosus* (after Habe 1943, fig. 5 *pars*).

Fig. 3. The central tooth of *Heliacus dorsuosus* (after Habe 1943, fig. 5 *pars*).

Fig. 4. A lateral tooth, in side view of *Philippia radiata* (after Robertson 1970, fig. 9C).

Fig. 5. Central tooth, in frontal view of *Philippia radiata* (after Robertson 1970, fig. 9D).

Fig. 6. Central tooth, in lateral view of *Philippia radiata* (after Robertson 1970, fig. 9B).

Fig. 7-10. Radula of *Architectonica reevei* (after Climo 1975, fig. 4B). Fig. 7. Front view of central tooth. Fig. 8. Lateral view of central tooth. Fig. 9. Lateral view of inner lateral tooth. Fig. 10. Lateral view of outer lateral tooth.

Figs. 11-14. Radula fo *Philippia oxytropis* (after Climo 1975, fig. 4A). Fig. 11. Outer lateral tooth. Fig. 12. Inner lateral tooth. Fig. 13. Frontal view of central tooth. Fig. 14. Lateral view of central tooth.

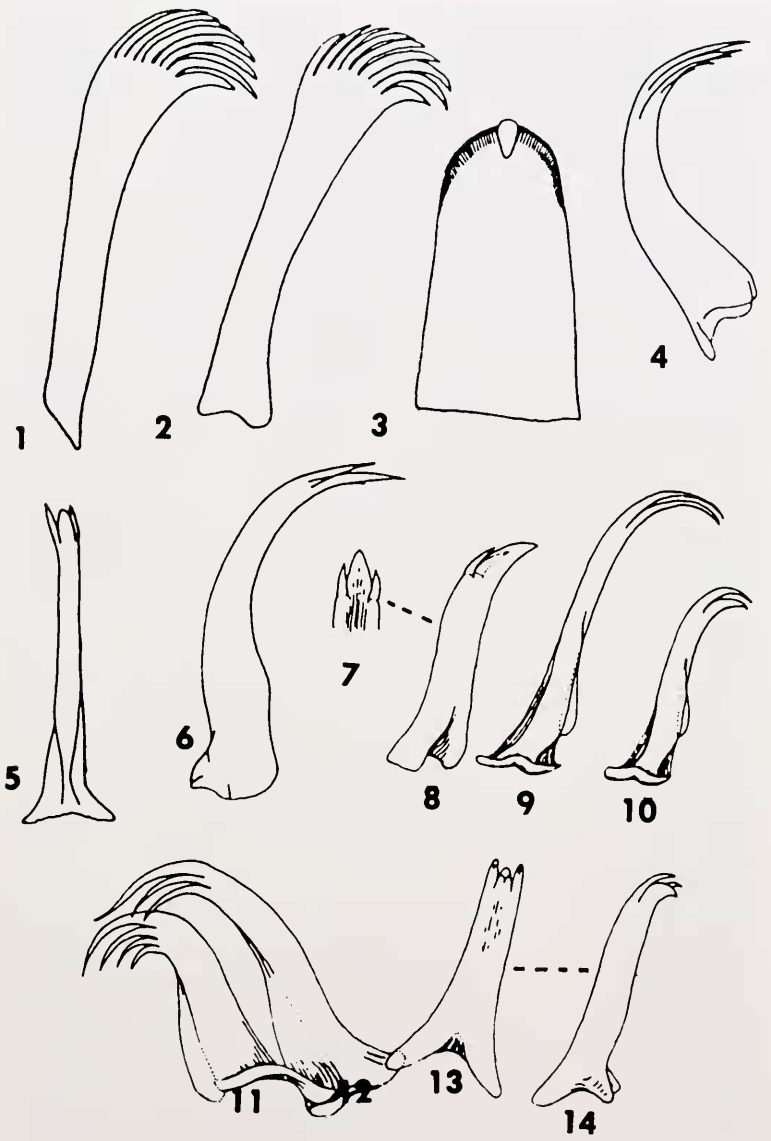

Plate 49

Plate 50. Portion of the radula of *Philippia hybrida*. a = outer lateral tooth. b = inner lateral tooth. c = central tooth. (Courtesy of G. Melone).
Fig. 1. 1000 ×
Fig. 2. 2000 ×

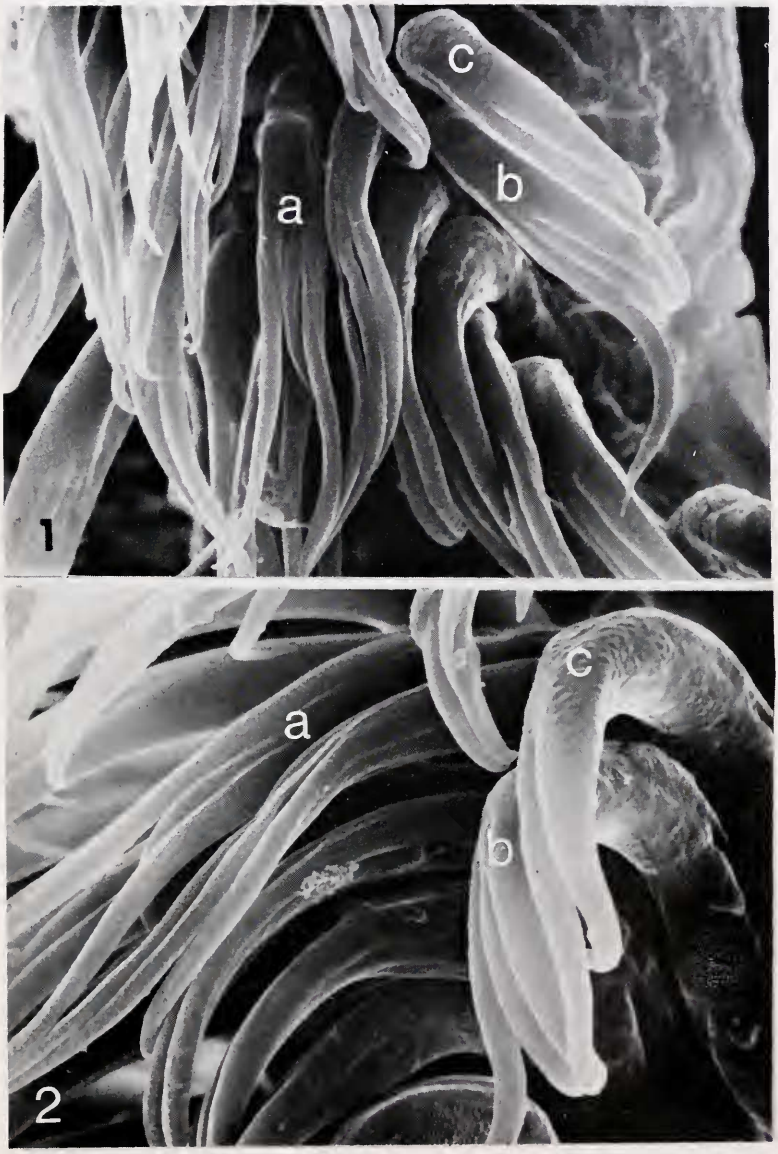

Plate 50

Plate 51. Portion of the radula of *Heliacus architae*. a = outer lateral tooth. b = inner lateral tooth. c = central tooth. (Courtesy of G. Melone).
Fig. 1. 2000 ×
Fig. 2. 5000 ×

Plate 51

Plate 52. Portion of the radula of *Heliacus fallaciosus*. a = outer lateral tooth. b = inner lateral tooth. c = central tooth. (Courtesy of G. Melone).
Fig. 1. 1000 ×
Fig. 2. 2000 ×

Plate 52

Plate 53. Portion of the radula of *Acutitectonica lepida* a = outer lateral tooth. b = inner lateral tooth. c = central tooth. (Courtesy of G. Melone).
Fig. 1. 500 ×
Fig. 2. 1000 ×

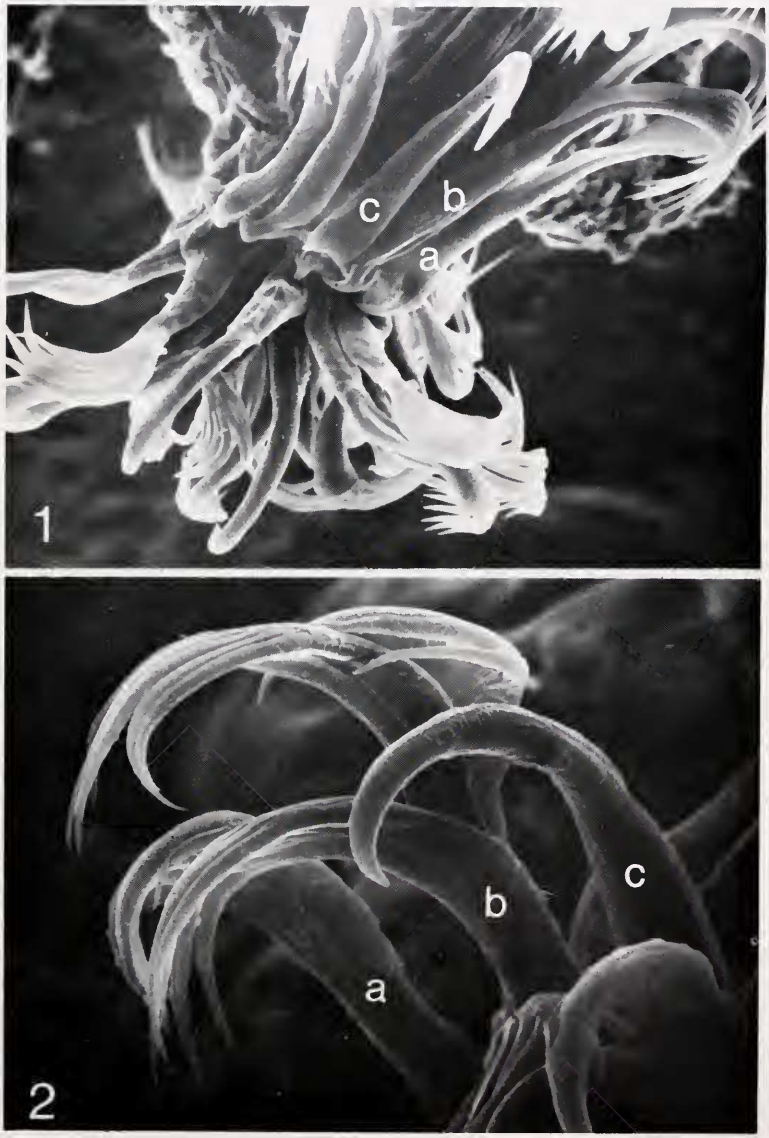

Plate 53

Plate 54. The accessory cuticularized rod-like structure from the esophagus of *Acutitectonica acutissima* (after Melone 1975).

Fig. 1. The structure aligned to show rows of double pairs of recurved elements (200 ×).

Fig. 2. The same enlarged to show recurved elements in greater detail (1000 ×). L = Lateral element. M = Medial element.

Fig. 3. The same viewed from a different angle (1000 ×). L = Lateral element. M = Medial element.

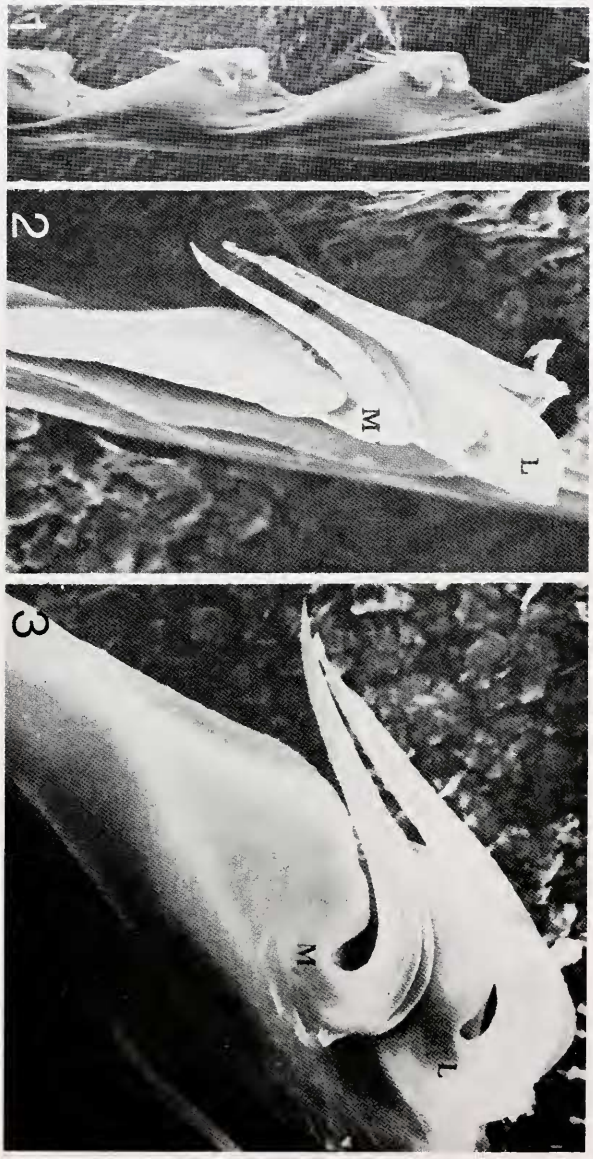

Plate 54

Plate 55

Fig. 1 The accessory cuticularized rod-like structure from the esophagus of *Acutitectonica disca* from El Colorado, Sonora, West Mexico in 80 fathoms. (40 ×). (about 4 mm in length).

Fig. 2. The same enlarged to show rows of double pairs of recurved elements (200 ×).

Fig. 3. The same enlarged to show recurved elements in greater detail (1500 ×).

Fig. 4. The same viewed from a different angle (1500 ×).

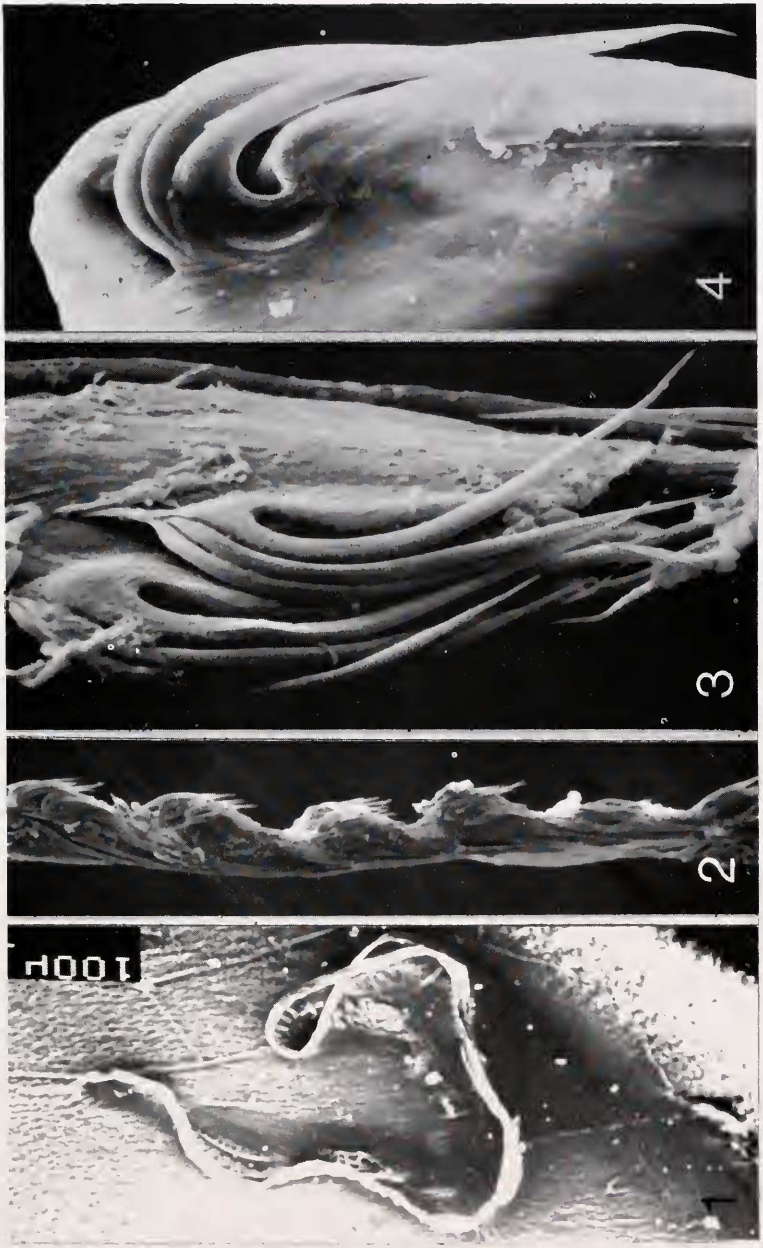

Plate 55

Plate 56

Fig. 1. *Architectonica perspectiva*. Kiwengwa, NE Zanzibar (ANSP); maximum diameter 47.0 mm. a. Portion of cuticularized esophageal tube showing position of radula and jaws within. b. Elements from portion of the jaw. c. Part of a single row of ptenoglossate radular teeth. d. Smallest lateral tooth observed. e. Largest tooth observed near the central part of a row of teeth.

Fig. 2. *Architectonica nobilis*. NE of Cape Kennedy, Florida (USNM); maximum diameter 48.5 mm. a. Portion of cuticularized esophageal tube and the entire buccal cavity showing position of radula and jaws within. b. Elements from portion of the jaw. c. Part of a single row of ptenoglossate radular teeth (figs. 2b, c, same scale).

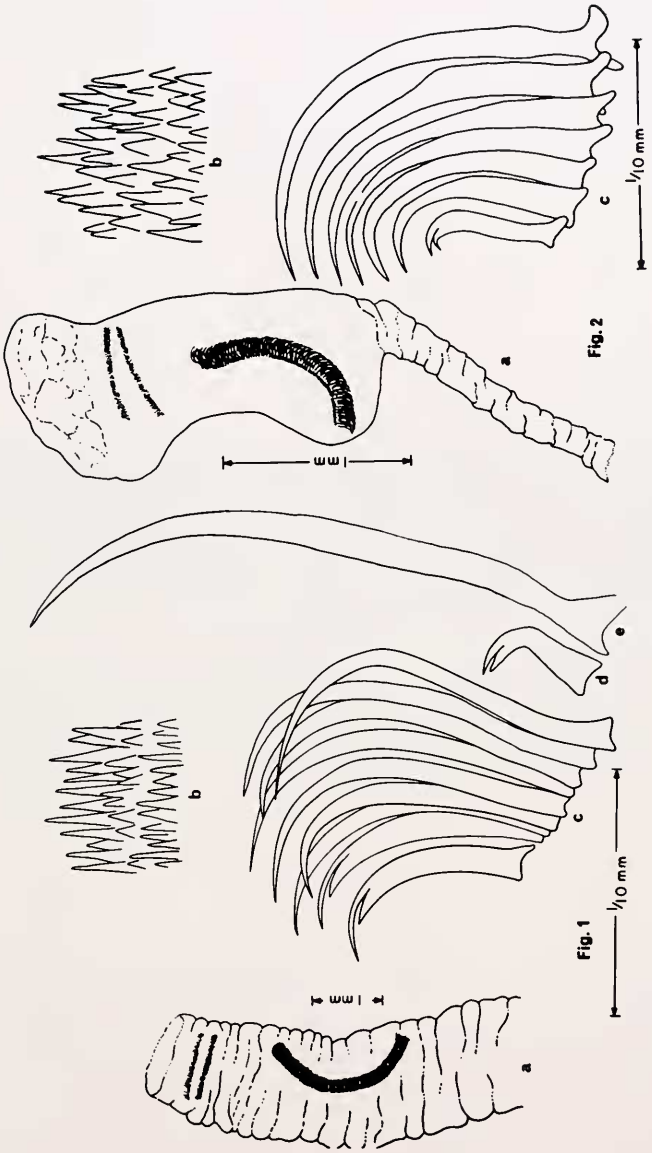

Plate 56

Plate 57

Fig. 1. *Philippia* (*Philippia*) *lutea*. Cape of Good Hope, Africa (USNM); maximum diameter 9.5. mm. a. Elements from portion of the jaw viewed obliquely from under the jaw. b. Entire radula and jaws within portion of cuticularized esophageal tube. c. Outline of the shape of a single row of teeth as viewed from the underside of the radular ribbon. d. Central (left) and two lateral radular teeth. e. Front and oblique views of central radular tooth. f. Side views of lateral teeth.

Fig. 2. *Philippia* (*Psilaxis*) *krebsii*. Castle harbor, Bermuda (MCZ); maximum diameter 5.5 mm. a. Elements from portion of the jaw. b. Front view of central radular tooth (left) and side view of two lateral teeth. c. Side view of central radular tooth (left) and two laterals. d. Front view of a complete central radular tooth.

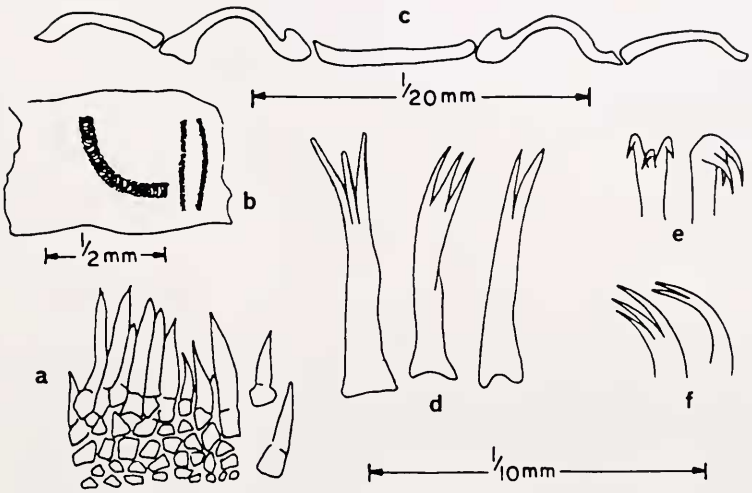

Fig. 1

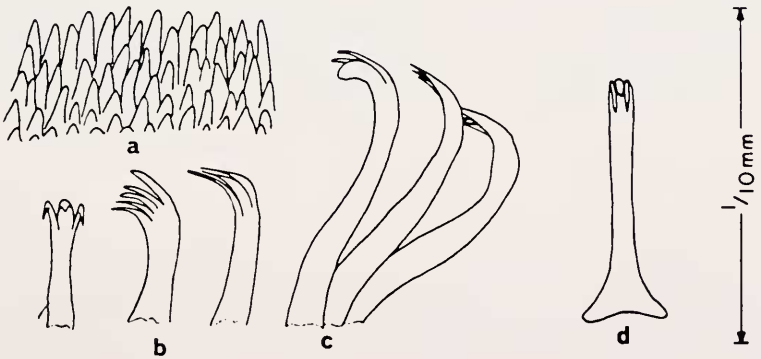

Fig. 2

Plate 57

Plate 58

Fig 1. *Acutitectonica disca.* W of Conakry, Guinea (UZM); maximum diameter 14.0 mm. a. Entire cuticularized buccal cavity including a portion of esophageal tube showing position of radula within the esophageal tube. b. Portion of jaw elements. c. Side views of central (left) and two lateral radular teeth. d. Side views of entire central radular tooth (left) and lateral tooth. e. Side views of lateral teeth to show varying number of cusps (figs. 1b, c, d, e, same scale).

Fig. 2. "Radula" of *Acutitectonica acutissima* (redrawn from Habe, 1952).

Fig. 3. Portion of peculiar cuticularized rod-like structure removed from the esophageal tube of *A. disca* with rows of recurved elements, two on each side of the rod or four to a row.

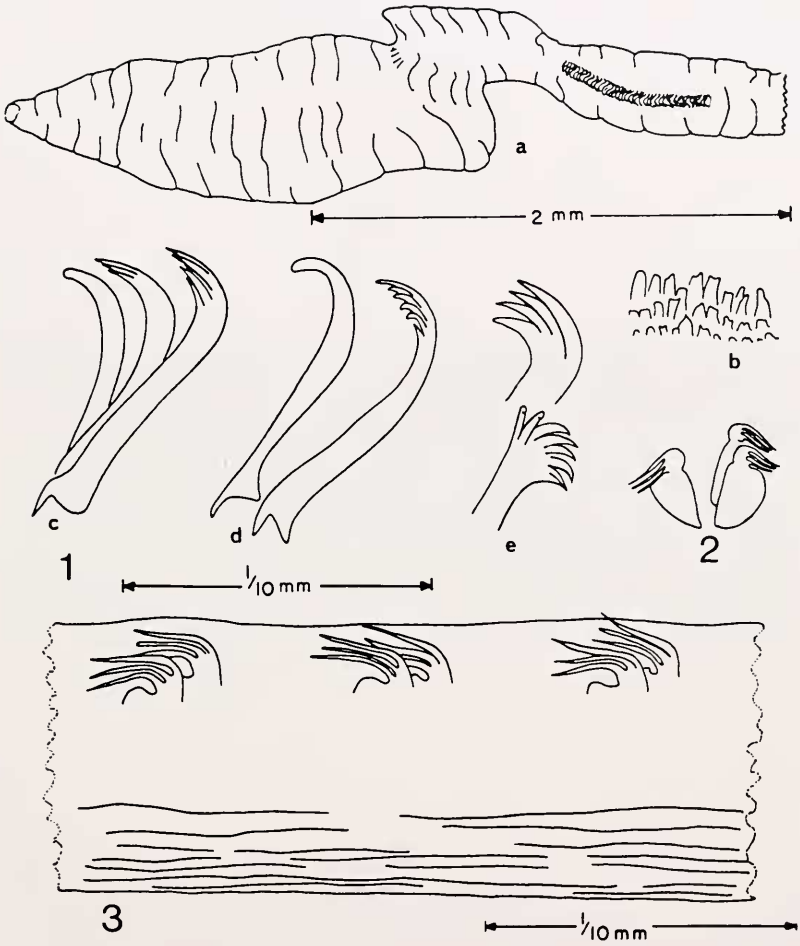

Plate 58

Plate 59

Fig. 1. *Heliacus* (*Heliacus*) *cylindricus*. Buccoo Reef and Bay, Tobago (ANSP); maximum diameter 10.6 mm. a. Portion of jaw elements. b. Front view of central radular tooth (left) and side view of two lateral teeth. c. Oblique view of central radular tooth.

Fig. 2. *Heliacus* (*Heliacus*) *perrieri*. Ragged Keys, Florida (MCZ); maximum diameter 16.1 mm. a. Portion of jaw elements. b. Position of jaws and radula in cuticularized esophageal tube. c. Front view of central radular tooth (right) and side view of two lateral teeth (note: cusps on either side of central knob are pressed out from the normal overlapping position—caused by pressure of cover slide). d. Side view of two lateral teeth. e. Front (left) and side views of two lateral teeth (cusps in lateral tooth, front view, pressed out similar to central tooth in fig. 2c).

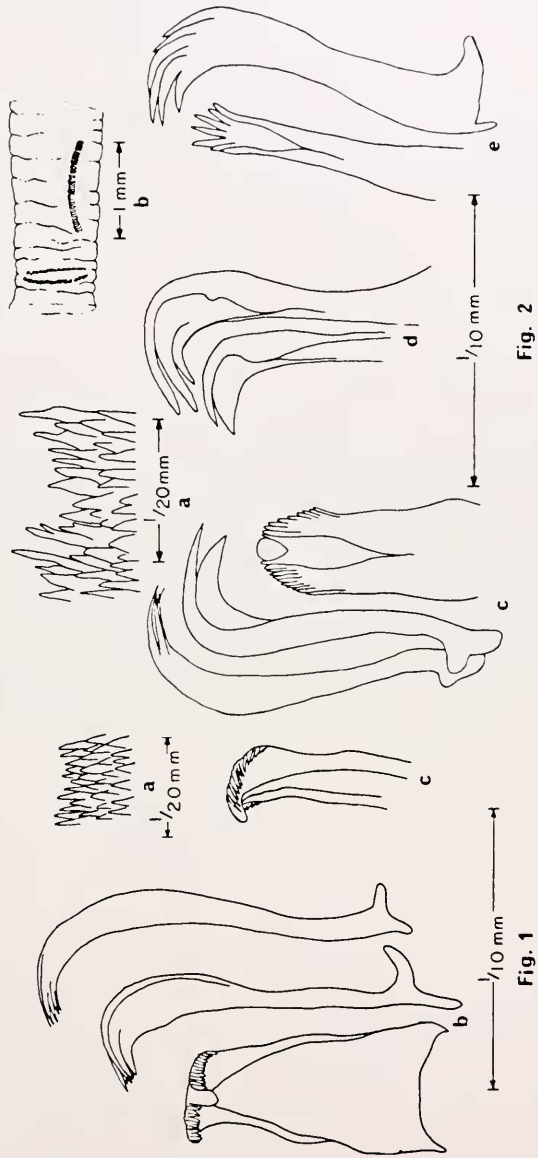

Plate 59

Plate 60

Fig. 1. *Heliacus* (*Gyriscus*) *jeffreysianus*. Sardinia, Italy (USNM); maximum diameter 8.7 mm. a. Front view of central radula tooth (left) and oblique view of two lateral teeth. b. Front (top) and side views of central radular tooth (note: cusps in lower central tooth pressed out by pressure of cover slide). c. Front (left) and side views of lateral teeth.

Fig. 2. *Heliacus* (*Solatisonax*) *borealis*. N of Iraconbo, French Guiana (BCF); maximum diameter 13.5 mm. a. Portion of jaw elements. b. Side view of complete radular (note regular spacing of the individual rows on the odontophore). c. Front view of portion of central radular tooth (left) and side view of portion of lateral tooth. d. Side view of central radular tooth (left) and two lateral teeth.

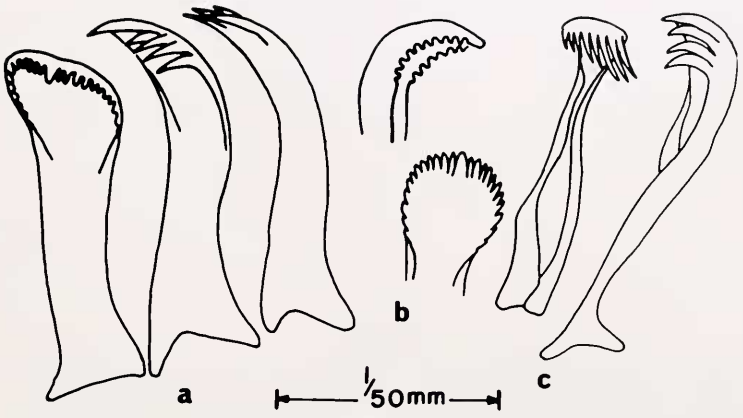

Fig. 1

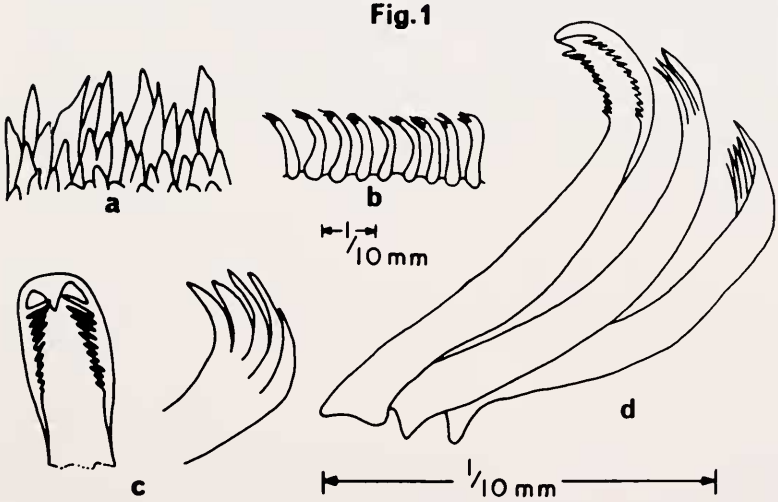

Fig. 2

Plate 60

Plate 61

Fig. 1. *Heliacus* (*Pseudotorinia*) *bisulcatus*. Off Government Cut, Miami, Florida (USNM); maximum diameter 4.8 mm. a. Oblique front view of central (left) and two lateral radular teeth. b. Portion of jaw elements. c. Front view of central radular tooth (left), side (right top) and front view of lateral teeth.

Fig. 2. *Heliacus* (*Pseudotorinia*) *architae*. Gulf of Naples, Italy (USNM); maximum diameter 3.8 mm. a. Front view of central radular tooth. b. Oblique view (left) and side view of lateral teeth. c. Side view of central radular tooth.

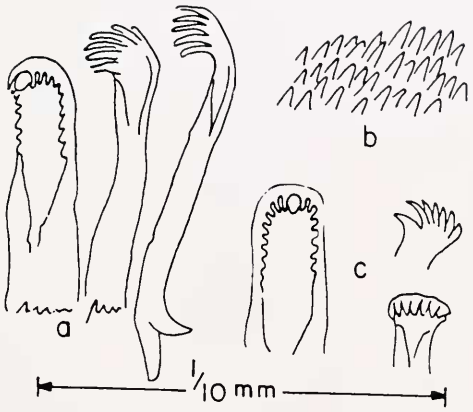

Fig. 1

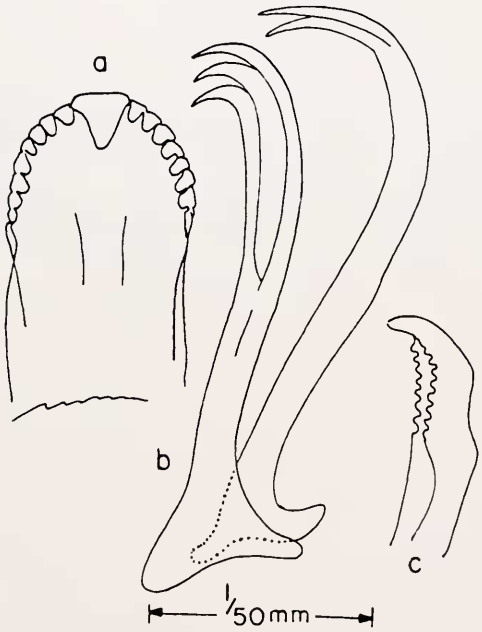

Fig. 2

Plate 61

Plate 62

Fig. 1. *Pseudomalaxis nobilis*. SE of Egmont Key, Florida (USNM): maximum diameter 11.2 mm. a. Side view of central radula tooth (left) and two lateral teeth. b. Front (bottom) and side (top) views of central radular tooth. c. Side view of lateral teeth.

Fig. 2. *Spirolaxis centrifuga*. Madeira (USNM); maximum diameter 3.2 mm. a. Portion of jaw elements. b. Front view of central and two lateral radular teeth. c. Side view of two lateral teeth.

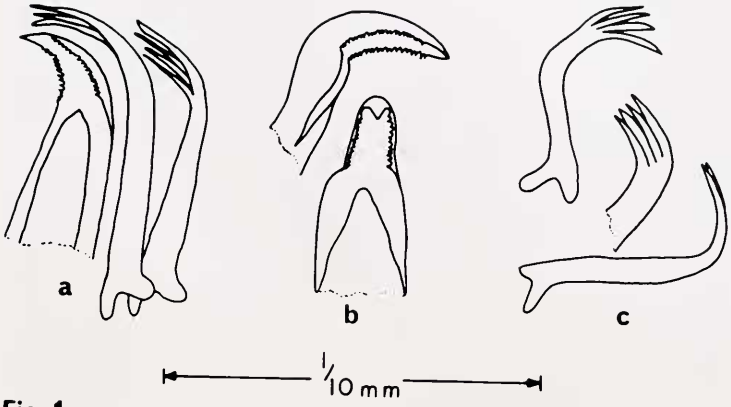

Fig. 1

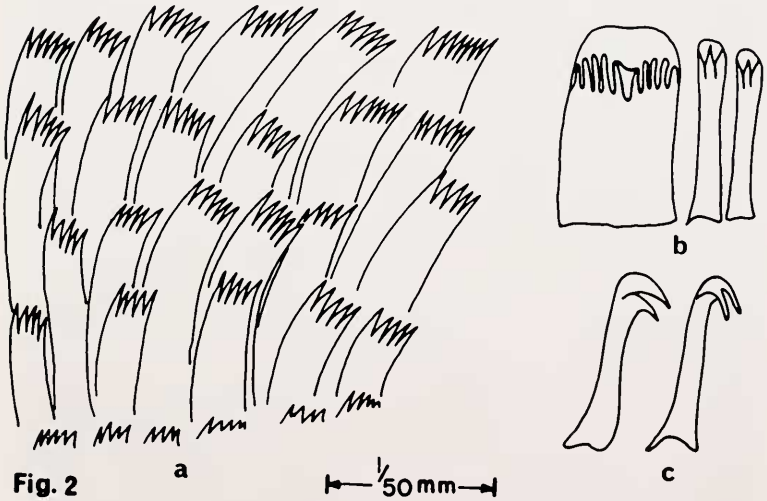

Fig. 2

Plate 62

Plate 63

Fig. 1. Portion of the radula of *Architectonica nobilis* from Brazil showing some rows of teeth with the more marginal lateral teeth being bicuspid, the more medial lateral teeth single pronged and the absence of a discernable central tooth (650 ×).

Fig. 2. Portion of a row of radular teeth of *Architectonica perspectiva* from between Du Rowa and Kai Dulah Is., Kai Islands, Moluccas, Indonesia (USNM 747000) showing bicuspid marginal lateral teeth at far right (660 ×).

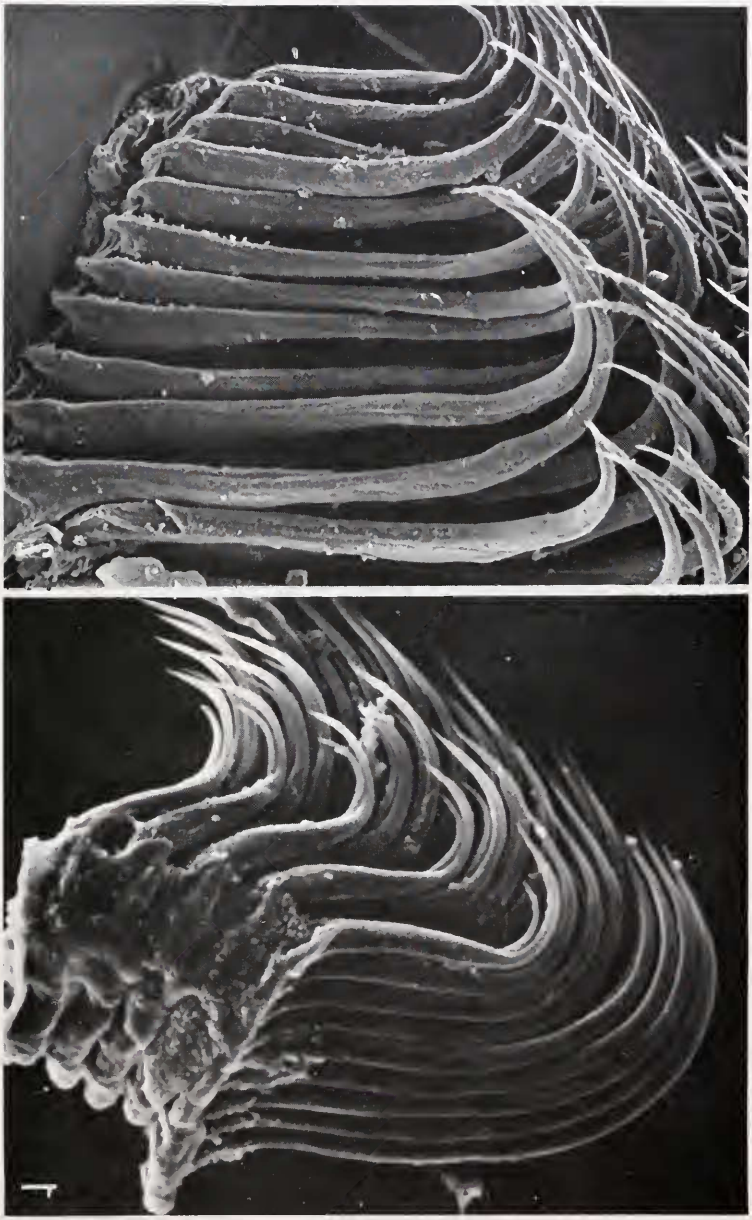

Plate 63

Plate 64. The radular of *Architectonica perspectivum* from between Du Rowa and Kai Dulah Is., Kai Islands, Moluccas, Indonesia (USNM 747000).

Fig. 1. Portion of radula showing entanglement of individual teeth (230 ×). Circle indicates area of enlargement in fig. 3.

Fig. 2. Enlargement of central field showing absence of anything distinguishable as a central tooth (800 ×).

Fig. 3. Enlargement of circled area of fig.1 to show bicuspid teeth (a) (1700 ×).

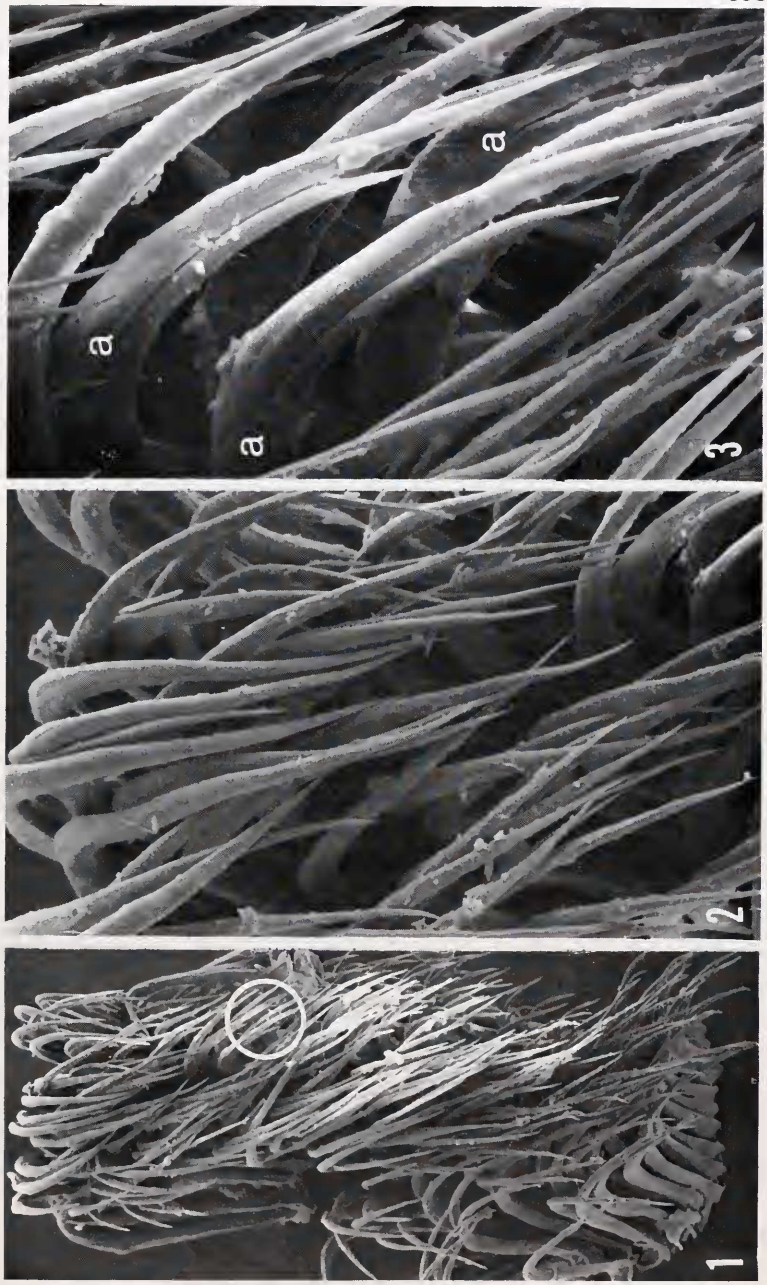

Plate 64

Plate 65

Fig. 1. Portion of radular ribbon of *Architectonica nobilis* from M/V *Silver Bay* Sta. 2399 (160 ×) showing central field somewhat spread open.

Fig. 2. Enlargement of circled area of fig. 1 showing two hooked teeth of central portion of the radula (1700 ×).

Fig. 3. The central tooth of *Philippia hybrida* from Sicily (2750 ×).

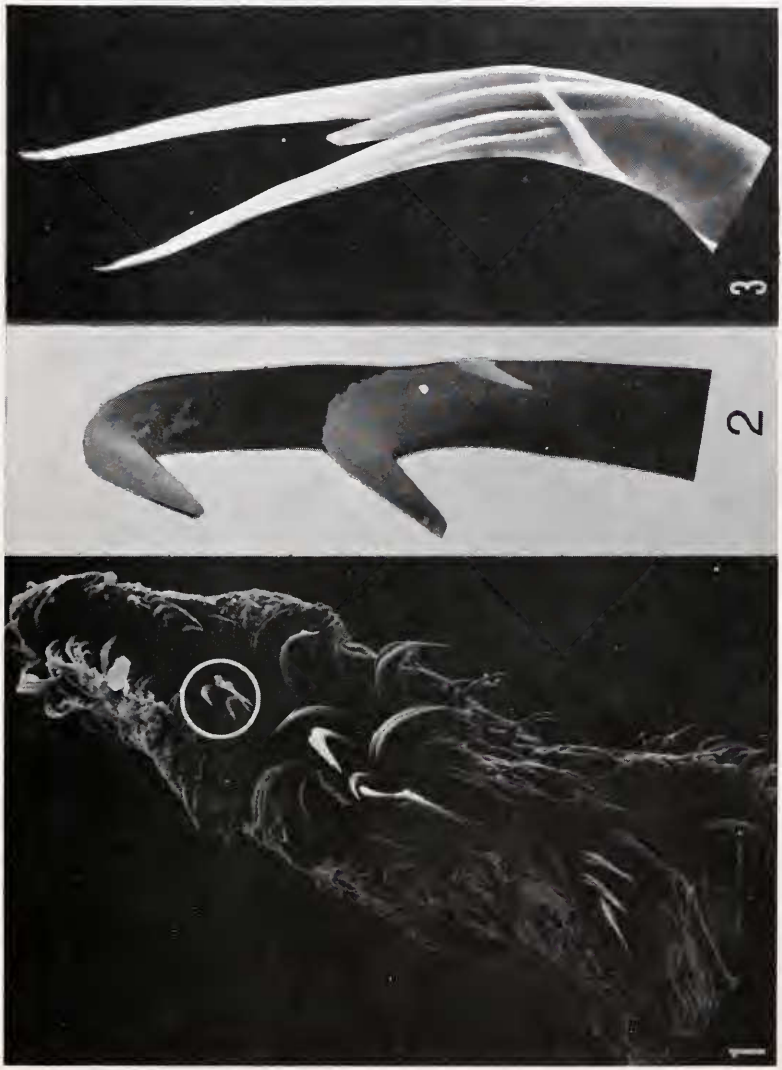

Plate 65

Plate 66. The radula of *Architectonica c.f. laevigata* from near Trangan, Aru, Moluccas, Indonesia (USNM 747441). a = Lateral tooth. c = Central tooth.

Fig. 1. Whole mount of the radula (240 ×).

Fig. 2. Rows of radular teeth showing individual central teeth and bicuspid lateral teeth (800 ×).

Fig. 3. Enlargement of rows of radula to show single pronged central tooth and bicuspid lateral teeth with seven on each side (1000 ×).

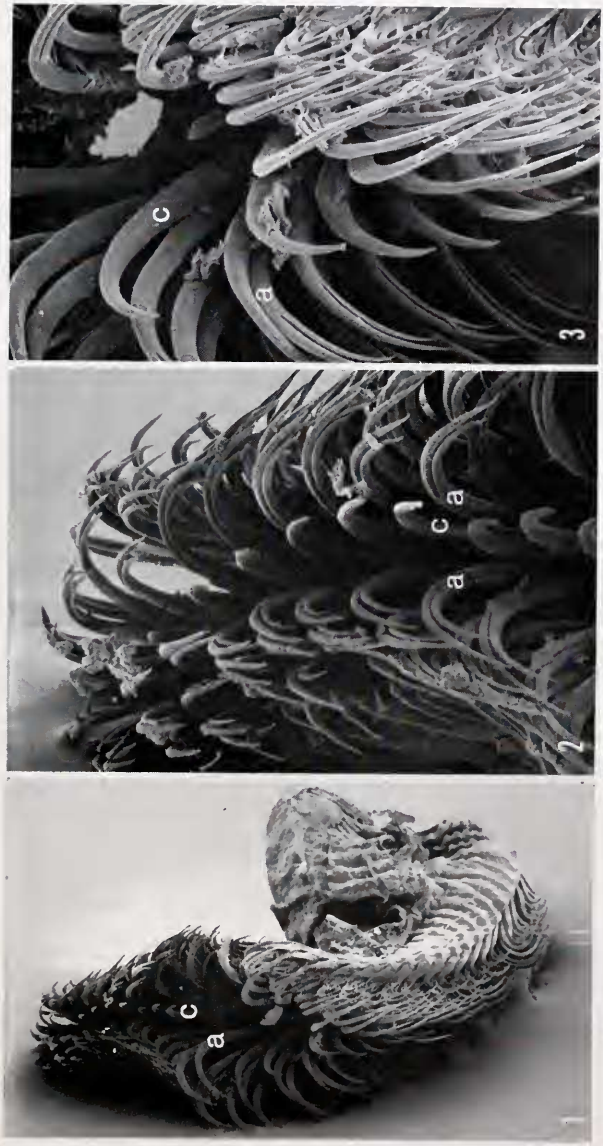

Plate 66

Plate 67

Fig. 1. Portion of the upperside of the distal edge of the jaw of *Architectonica nobilis* from Brazil to show pointed tips of the jaw elements (about 2200 ×).

Fig. 2. Portion of the underside of the jaw of *A. nobilis* to show hexagonal pattern of base of jaw elements (about 2800 ×).

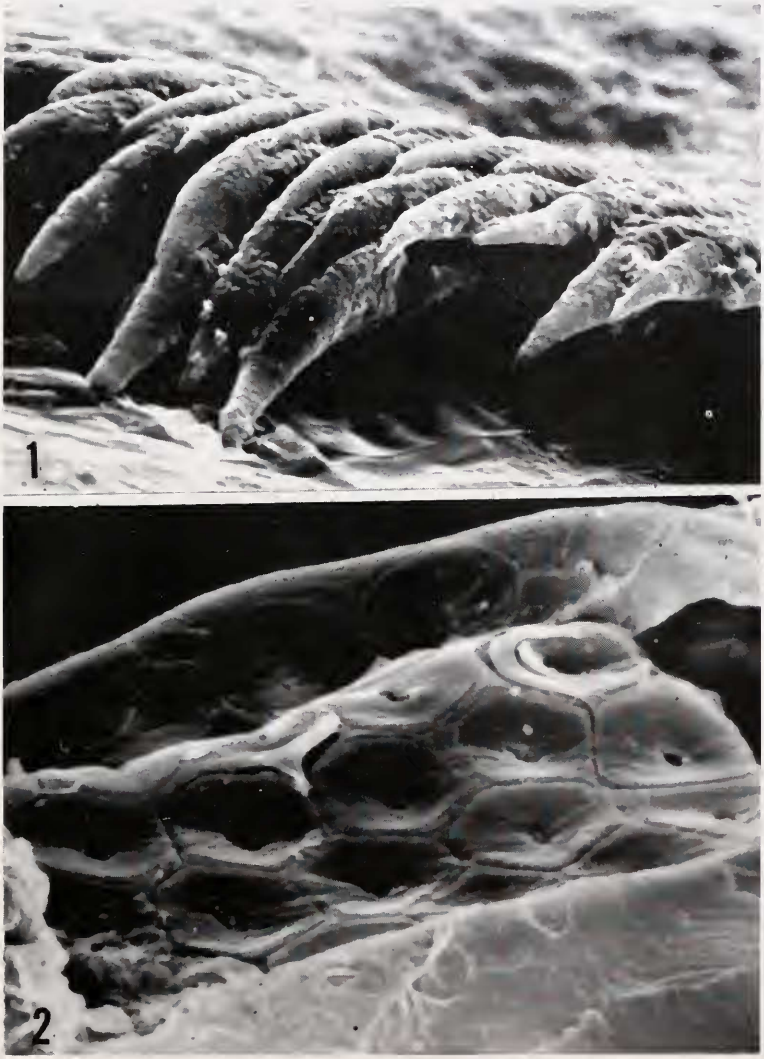

Plate 67

Plate 68

Fig. 1. Portion of the upperside of the distal edge of the jaw of *Philippia hybrida* from Sicily (USNM) to show incised pointed tips of the jaw elements (2000 ×).

Fig. 2. Portion of the underside of the jaw of *P. hybrida* to show papillose bulbous bases of jaw elements (2000 ×).

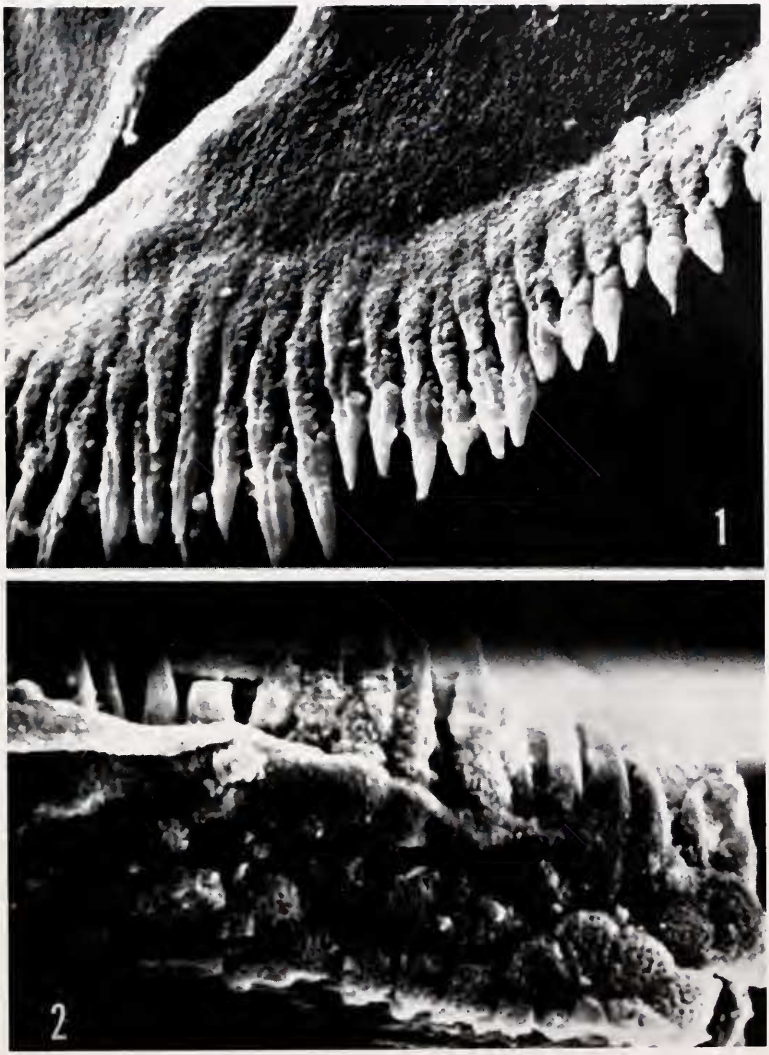

Plate 68